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SYSTEMATIC STUDIES AND CONSERVATION STATUS OF *CLAYTONIA LANCEOLATA* VAR. *FLAVA* (PORTULACACEAE)

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ABSTRACT

A biosystematic study of *Claytonia lanceolata* and related taxa in the Rocky Mountains was undertaken to evaluate the taxonomic status of *C. lanceolata* var. *flava*. This study was part of a broader assessment to determine the need for protection of the latter taxon under the federal Endangered Species Act. Electrophoretic and morphological studies revealed that *C. lanceolata* var. *flava* in southwestern Montana and northwestern Wyoming represents a distinct diploid species (n=8) whose populations consist of yellow- and/or white-flowered plants. Morphological, allozyme, and cytological data all indicate that this taxon does not belong in the *C. lanceolata* complex, but is best placed in the group of narrow-leaved species that includes *C. rosea, C. tuberosa,* and *C. virginica.* Numerous populations of *C. lanceolata* var. *flava,* most often consisting of the white-flowered phenotype, were found in Montana and Wyoming, and legal protection is not warranted at this time. In some cases, actions to conserve endangered plant taxa must be preceded by an evaluation of their taxonomic status; this study illustrates the utility of biosystematic techniques in conducting such evaluations.

INTRODUCTION

A need for accurate taxonomic evaluations of rare plant species has frequently arisen as conservation of biological diversity has become a priority on the part of government agencies and private organizations. Such evaluations are critical to ensuring that the limited funding available for plant conservation is devoted to taxa that are deserving from a biosystematic perspective.

Claytonia lanceolata Pursh (Portulacaceae) is a common, wide-ranging species of western North America (Hitchcock et al. 1964). *Claytonia lanceolata* var. *flava* (A. Nels.) C. L. Hitchc. has been applied to yellow-flowered populations in the northern Rocky Mountains (Hitchcock et al. 1964; Davis 1966). The type collection of this variant was made in 1899 by Aven and Elias Nelson (*5488,* RM), near the northwest corner of Henry's Lake in Fremont County, Idaho (Nelson 1900). From 1911 to 1988, it was collected at five additional stations in southwestern Montana (Shelly 1989) and one station in northwestern Wyoming (Marriott 1986). It was rediscovered at the type locality in 1986 (D. Atwood personal communication). The infrequency of collection and the relatively restricted geographic range of these yellow-flowered populations led to the designation of *C. lanceolata* var. *flava* as a candidate for listing under the federal Endangered Species Act (U.S. Fish and Wildlife Service 1985, 1993).

The taxon was initially described as *C. aurea* (Nelson 1900). Rydberg (1922) reduced this name to a synonym of *C. chrysantha* Greene (=*C. lanceolata* var. *chrysantha* (Greene) C. L. Hitchc., a yellow-flowered form of the latter species occurring in western Washington (Douglas and Taylor 1972)), undoubtedly based on the shared flower color. *Claytonia aurea* was later renamed *C. flava,* the former name having already been used by Kuntze in 1891 (Nelson 1926). Rydberg (1932) also subsequently recognized it as *C. flava.* Since that time, *C. flava* has been reduced to a variety of *C. lanceolata* on two separate occasions (Hitchcock et al. 1964; Davis 1966). The latter revision was perhaps an oversight of the Hitchcock treatment, and Davis has occasionally been cited as the author of this change. Boivin (1968) placed *C. flava* as a variety of *C. caroliniana* Michx. More recently, the taxon has again been treated as a species (Dorn 1984).

We conducted two studies to evaluate the need for listing of *C. lanceolata* var. *flava* under the federal Endangered Species Act. In the first study, we

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used isozyme electrophoresis and field morphological analyses to compare *C. lanceolata* var. *flava* with sympatric populations of *C. lanceolata* var. *lanceolata.* The purpose of this study was to assess the current taxonomic treatment of the yellow-flowered populations as a variety of the latter, common taxon. During initial field work, surveys of known Montana populations of *C. lanceolata* var. *flava* revealed the presence of narrow-leaved, white-flowered plants that were morphologically very similar to the yellow-flowered individuals. These white-flowered plants did not fit the descriptions of typically broader-leaved *C. lanceolata* var. *lanceolata.* Thus, we also examined the degree of isozyme differentiation between white- and yellow-flowered individuals of these narrow-leaved plants, and whether any other morphological differences aside from petal color exist between them. Yellow- and white-flowered individuals of these narrow-leaved plants are biotically sympatric, occurring in intermixed populations, in four of the five study locations. Furthermore, these narrow-leaved plants are either biotically or neighboringly sympatric (occurring in closely adjacent but non-overlapping populations) with *C. lanceolata* var. *lanceolata* in all five study locations.

In the second study, we undertook herbarium morphological analyses in an initial attempt to place the narrow-leaved *Claytonia* populations of the northern Rocky Mountains in a broader context with respect to other congeneric taxa. In addition to *C. lanceolata* vars. *flava* and *lanceolata,* other taxa included in this herbarium study were *C. lanceolata* var. *chrysantha* (Greene) C. L. Hitchc., *C. lanceolata* var. *multiscapa* (Rydb.) C. L. Hitchc., and *C. rosea* Rydb. This second study did not include electrophoretic analyses, as it was intended to be a preliminary assessment of the wider affinities of *C. lanceolata* var. *flava* within the narrow-leaved *Claytonia*s.

The taxonomy of *Claytonia* is currently being revised for the Flora of North America project (Miller and Chambers in mss.). Pending publication of this treatment, throughout this paper the name *C. lanceolata* var. *flava* will refer to populations of both the white and yellow flower color phenotypes of the narrow-leaved taxon, except when citing previous alternative treatments.

Materials and Methods

Five populations of *C. lanceolata* var. *lanceolata* and seven of var. *flava* (four consisting of plants with both yellow and white flowers, two including only white-flowered plants, and one consisting of only yellow-flowered plants) were sampled for morphological and isozyme electrophoretic studies. All five populations of var. *lanceolata* were included in both studies. For var. *flava,* five of the seven populations were included in both studies; the two exceptions were the Boulder and Burton Park populations (consisting of only the white-flowered phenotype in both cases), which we were unable to include in the electrophoretic analysis. The study populations are located in southwestern Montana and northwestern Wyoming (Fig. 1, Table 1).

Morphological studies. Morphological studies were conducted with live plants in the field and with herbarium specimens. We emphasized characters that are easily examined on living plants and pressed specimens, and that have been used in past keys treating some or all of the taxa of interest.

In the field, morphological data were collected from 720 living plants, representing five populations of *C. lanceolata* var. *lanceolata* and seven populations of var. *flava* (four including both yellow- and white-flowered plants, two with white-flowered plants only, and one with yellow-flowered plants only). In each population (and for each color phenotype in the mixed populations of var. *flava*), 45 plants were examined for the following characters: stem height, leaf length and width, petal length and width, and sepal length. Stem height was measured in centimeters, from ground level to the point of attachment of the uppermost pedicel; all other lengths were measured in millimeters. For statistical analyses, length/width ratios of the leaves and petals were also calculated.

One hundred eighty-four herbarium collections, representing *C. lanceolata* vars. *lanceolata, flava, multiscapa,* and *chrysantha,* as well as *C. rosea,* were examined from the following herbaria: MONTU, OSC, RM, UA, UAL, WS, WTU. In addition to the characters listed above, the petal/sepal length was calculated, and petal apex outline and cauline leaf venation were scored for the herbarium specimens (see Table 4 for scoring criteria).

Isozyme Electrophoresis. A total of 679 individuals from 10 populations (five of *C. lanceolata* var. *lanceolata,* four of var. *flava* consisting of both the yellow- and white-flowered phenotypes, and one strictly yellow-flowered population of the latter) was sampled. Both color phenotypes were sampled in the mixed populations of var. *flava.* Whole flowering stems, including the cauline leaves, were collected by clipping the plants at ground level. These were kept chilled in the field for one to several days until placement in ultracold storage (−80°C).

Leaves were ground immediately upon removal from the ultracold freezer, in the Tris HCl-PVP crushing buffer of Soltis et al. (1983) with 6% PVP. Nineteen putative loci, coding for twelve enzymes, were resolved using three electrophoretic buffers. A morpholine buffer, pH 6.4 (Odrzykoski and Gottlieb 1984) was used to resolve glyceraldehyde-3-phosphate dehydrogenase (G3PDH), malate dehydrogenase (MDH), and phosphoglucomutase (PGM). Buffer 8 of Soltis et al. (1983), as modified by Haufler (1985), was used to resolve alcohol dehydrogenase (ADH), aspartate aminotransferase (AAT), leucine aminopeptidase (LAP), phospho-

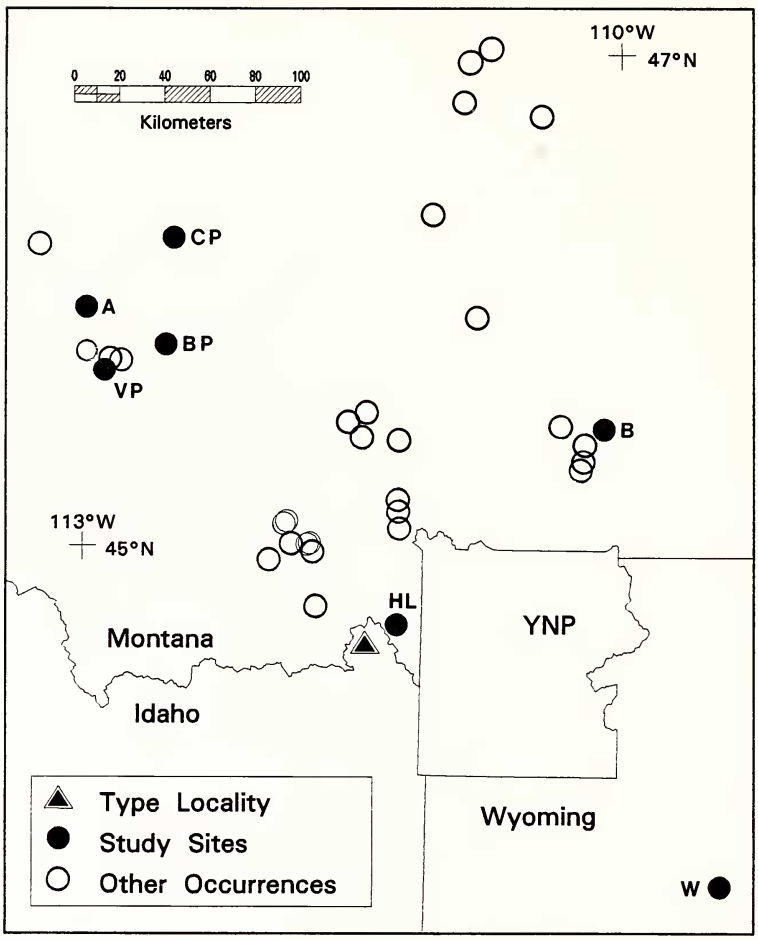

FIG. 1. Distribution of *Claytonia lanceolata* var. *flava* in Montana, Idaho and Wyoming, and locations of study populations (A = Anaconda; B = Boulder; BP = Burton Park; CP = Champion Pass; HL = Hebgen Lake; VP = Vipond Park; W = Wyoming; YNP = Yellowstone National Park). Open circles indicate additional occurrences of yellow- and/or white-flowered populations, as recorded by the Montana Natural Heritage Program; the type locality, in Idaho, has only been observed to contain yellow-flowered individuals.

glucoisomerase (PGI), and triosephosphate isomerase (TPI). Buffer 11 of Soltis et al. (1983) was used to resolve isocitrate dehydrogenase (IDH), menadione reductase (MNR), shikimate dehydrogenase (SkDH), and 6-phosphogluconate dehydrogenase (6PGD). The stain recipe for ADH was that described by Wendel and Weeden (1989). All other staining protocols were those of Soltis et al. (1983).

Data analysis. We assessed the morphological distinctiveness of the taxa using principal components analysis (PCA) and discriminant analysis of the characters listed above. These analyses were performed using SYSTAT (Wilkinson 1986), and were based on log-transformed values for the characters listed above.

Electrophoretic data were analyzed using the computer program BIOSYS-1 (Swofford and Selander 1981). Two separate analyses were performed: 1) allele frequencies at 19 loci were entered for all ten populations (14 samples total, since both color phenotypes were included from the four mixed populations of var. *flava*) and analyzed for genetic variability statistics and Nei's genetic identity between populations of *C. lanceolata* vars. *lanceolata* and *flava,* and between the nine populations of var. *flava* (five yellow- and four white-flowered); and 2) eight *C. lanceolata* var. *flava* populations, from all localities except Hebgen Lake (yellow-flowered phenotype only), were entered as genotype numbers and analyzed for population substructuring, to examine differences between color phenotypes within localities. An unweighted pair group method (UPGMA) was used for cluster analysis of Nei's genetic identity relationships.

RESULTS

Field studies. Taxon means, ranges, and standard deviations for the eight quantitative characters measured on living plants are given in Table 2.

TABLE 1. POPULATIONS OF *CLAYTONIA LANCEOLATA* VARS. FLAVA AND LANCEOLATA ANALYZED IN ISOZYME AND FIELD MORPHOLOGICAL STUDIES. Flower color phenotypes of var. *flava* were sampled as separate "populations" where they are biotically sympatric (Anaconda, Champion Pass, Vipond Park, and Wyoming). Vouchers are deposited at MONTU; * = duplicates deposited at OSC. + = the Boulder and Burton Park populations of white-flowered *flava* were not included in the electrophoretic study.

Taxon	Abbreviation	Collection data
Claytonia lanceolata var. *flava*	ANACONDA WHITE	Montana, Deer Lodge Co. *Shelly & Lesica 1412**
	ANACONDA YELLOW	Montana, Deer Lodge Co. *Shelly & Lesica 1413**
	BOULDER WHITE+	Montana, Sweet Grass Co. *Shelly 1617*
	BURTON PARK WHITE+	Montana, Silver Bow Co. *Shelly, Schassberger & Schitoskey 1504*
	CHAMPION YELLOW	Montana, Jefferson Co. *Shelly 1417**
	CHAMPION WHITE	Montana, Jefferson Co. *Shelly & Lesica 1423**
	HEBGEN YELLOW	Montana, Gallatin Co. *Shelly & Lesica 1419**
	VIPOND YELLOW	Montana, Beaverhead Co. *Shelly & Scow 1444**
	VIPOND WHITE	Montana, Beaverhead Co. *Shelly & Scow 1445**
	WYOMING YELLOW	Wyoming, Fremont Co. *Shelly & Lesica 1446**
	WYOMING WHITE	Wyoming, Fremont Co. *Shelly & Lesica 1447**
Claytonia lanceolata var. *lanceolata*	ANACONDA LANCEO	Montana, Deer Lodge Co. *Shelly & Lesica 1411*
	CHAMPION LANCEO	Montana, Jefferson Co. *Shelly & Lesica 1422*
	HEBGEN LANCEO	Montana, Madison Co. *Shelly & Lesica 1420**
	VIPOND LANCEO	Montana, Beaverhead Co. *Shelly 1201*
	WYOMING LANCEO	Wyoming, Teton Co. *Shelly & Lesica 1448**

PCA of the living-plant morphological characters other than flower color revealed that white-flowered and yellow-flowered forms of *C. lanceolata* var. *flava* are indistinguishable from each other but are easily separable from *C. lanceolata* var. *lanceolata* (Fig. 2). The first principal component accounted for 46% of the variation and had strong contributions by petal width, leaf length, stem height, leaf length/width ratio, sepal length, and petal length/width ratio. The second component had strong loadings by leaf width and petal length and accounted for 20% of the variation (Table 3).

The cross-validation error rate for the discriminant analysis comparing white- and yellow-flowered individuals of *C. lanceolata* var. *flava* was 0.42; there is only a 58% chance of correctly identifying the two flower color phenotypes of *C. lanceolata* var. *flava* based on the morphological characters used in the analysis. Thus, the two phenotypes cannot be reliably discriminated on characters other than flower color.

Herbarium studies. Taxon means, ranges, and standard deviations for the eight quantitative and two qualitative characters examined on the herbarium collections are given in Table 4.

PCA of the herbarium morphological characters other than flower color also revealed that white-flowered and yellow-flowered forms of *C. lanceolata* var. *flava* are indistinguishable from each other, and are very similar to var. *multiscapa* and *C. rosea,* but that specimens of all three latter taxa are easily separable from *C. lanceolata* var. *lanceolata* (including *C. lanceolata* var. *chrysantha*; Fig. 3). The first principal component accounted for 33% of the variation and had strong contributions by leaf venation, petal apex outline, leaf length/width ratio, leaf width, petal/sepal length ratio, and sepal length. The second component had strong loadings by petal width and length and accounted for 22% of the variation (Table 5).

Isozyme electrophoresis. Coding of populations of *C. lanceolata* var. *flava* was straightforward, as

TABLE 2. TAXON MEANS, RANGES AND STANDARD DEVIATIONS FOR FIELD MORPHOLOGICAL DATA, *CLAYTONIA LANCEOLATA* VARS. FLAVA AND LANCEOLATA.

	Yellow *flava*	White *flava*	*lanceolata*
No. of specimens	225	270	225
Height (cm)			
Mean	7.6	9.6	4.1
Range	3.5–16.9	4.0–27.2	1.4–10.8
SD	2.1	1.3	1.5
Leaf length (mm)			
Mean	36.0	42.8	26.3
Range	13.0–76.0	14.0–111.0	14.0–46.0
SD	11.7	18.4	6.8
Leaf width (mm)			
Mean	5.4	5.9	9.1
Range	2.5–11.5	3.0–13.5	4.0–19.0
SD	1.6	1.9	2.7
Sepal length (mm)			
Mean	5.0	5.1	4.0
Range	3.0–8.5	3.5–8.0	2.0–6.0
SD	0.98	0.83	0.79
Petal width (mm)			
Mean	5.3	5.7	4.2
Range	3.0–8.5	3.0–9.0	2.5–9.0
SD	0.96	0.97	0.84
Petal length (mm)			
Mean	8.6	9.2	8.8
Range	6.0–12.0	6.5–13.5	4.5–12.5
SD	1.2	1.1	1.3
Leaf length/width ratio			
Mean	6.8	7.5	3.0
Range	3.3–14.2	2.6–18.5	1.6–6.3
SD	2.0	2.6	0.9
Petal length/width ratio			
Mean	1.7	1.6	2.1
Range	1.1–2.3	1.1–2.3	0.5–3.0
SD	0.2	0.2	0.3

simple diploid expression was observed in all cases. However, *C. lanceolata* var. *lanceolata* expressed more complex banding patterns indicative of tetraploidy. To make comparisons among varieties and flower-color phenotypes at each locality, it was necessary to code allele frequencies for *C. lanceolata* var. *lanceolata.* This was done by assuming that each individual was tetraploid and possessed four allelic doses per locus. Some individuals, therefore, expressed more than two alleles at a locus. Relative staining intensities were used to determine dosage effects (Wolf 1988). Allele frequencies are given in Table 6.

Differences between varieties. The UPGMA cluster analysis of Nei's genetic identity values is shown in Figure 4. All five populations of *C. lanceolata* var. *lanceolata* were completely separated from the nine populations of *C. lanceolata* var. *flava* (represented by samples of both white- and yellow-flowered plants). The mean genetic identity between populations of these two taxa was 0.69.

Differences among populations of C. lanceolata var. *flava.* The UPGMA cluster analysis also indicates the level of differentiation among populations of *C. lanceolata* var. *flava* (Fig. 4). With the color phenotypes pooled within localities, genetic identity values among the five study localities ranged from 0.913 to 0.979. The genetic identities correspond to geographic proximity; the more southerly populations (Hebgen Lake and Wyoming) clustered together, as did the northern populations (Anaconda, Champion, and Vipond).

Differences between color phenotypes within localities of C. lanceolata var. *flava.* In the four cases where they are biotically sympatric, yellow- and white-flowered "populations" of *C. lanceolata* var. *flava* were always more similar allozymically to each other than to allopatric populations of the same flower color (Fig. 4). The Nei's genetic identity values between color phenotypes within localities were high, ranging from 0.995 (Vipond Park) to 1.00 (Anaconda). By contrast, interpopulation genetic identity values within color phenotypes ranged from 0.935 to 0.987 for the yellow form, and from 0.910 to 0.989 for the white form.

DISCUSSION

Morphological studies and isozyme electrophoresis revealed that populations ascribed to *C. lanceolata* var. *flava* represent a diploid species ($2n=16$; Marriott 1986) that is distinct from the *C. lanceolata* complex. *Claytonia lanceolata* displayed banding patterns suggestive of autopolyploidy in the populations we sampled. Tetraploid populations ($n=16$) of *C. lanceolata* have been reported from Utah (Halleck and Wiens 1966; Stewart and Wiens 1971), and populations with $n=8$, 12, 18, 22, 24, and 32 have been found in other Rocky Mountain populations of this species (Davis and Bowmer 1966; Halleck and Wiens 1966).

In past treatments, petal color, described as "golden yellow" by Davis (1952, 1966) and "deep yellowish-orange" by Hitchcock et al. (1964), was the primary character used to distinguish *C. lanceolata* var. *flava* from related taxa at the level of species (as *C. flava*; Davis 1952) or variety (Hitchcock et al. 1964; Davis 1966). However, PCAs of our morphological data indicated that the characters most important for distinguishing *C. lanceolata* var. *flava* from typical *C. lanceolata* are related to leaf morphology (length/width ratio and venation) and petal shape (length/width ratio and apex outline).

Davis (1952) described the leaves of *C. lanceolata* var. *flava* as "linear or lance-linear," as compared to "stem leaves lanceolate" in *C. lanceolata.* Similarly, Hitchcock et al. (1964) described the stem leaves of *C. lanceolata* var. *flava* as "lanceolate or narrowly oblong, several times longer than broad" and those of *C. lanceolata* (represented by

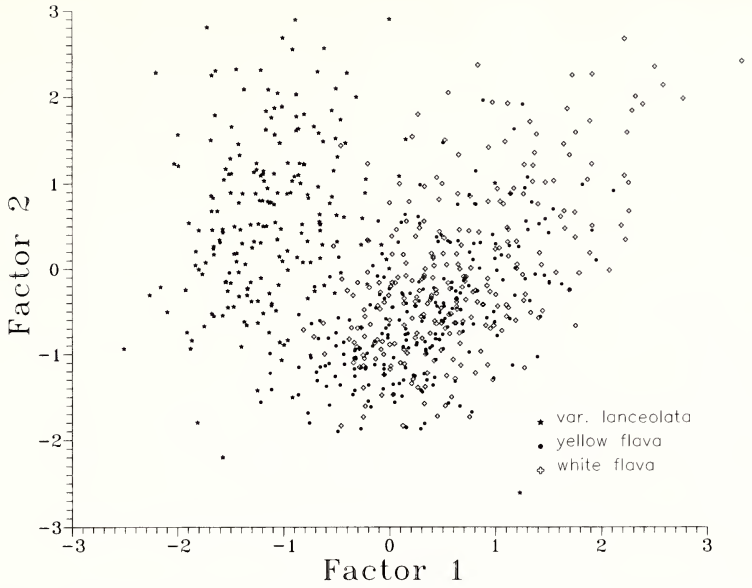

FIG. 2. Scatter diagram of individuals of *Claytonia lanceolata* var. *flava* (yellow- and white-flowered) and *C. lanceolata* var. *lanceolata* on principal components 1 and 2. Based on morphological data collected from living plants in the field.

var. *chrysantha*) as "broadly elliptic to ovate, (1)1.5–2.5(4) cm long, usually over ⅓ as broad." Our study showed that the leaves of *C. lanceolata* var. *flava* average approximately seven times longer than wide, whereas those of typical *C. lanceolata* average three times as long as wide (Table 2). These numeric differences are in accordance with the earlier, largely qualitative leaf shape differences described for these taxa.

Rydberg (1922) recognized the patterns in leaf venation that distinguish the narrow-leaved species of *Claytonia* (i.e., *C. virginica, C. rosea,* and *C. multiscapa*) from *C. lanceolata.* He observed that the former group has leaves "1-ribbed or indistinctly 3-ribbed," whereas the latter species has leaves that are "distinctly triple-ribbed." Our results uphold this as a valid and important means of distinguishing the narrow-leaved *Claytonia* populations from those of *C. lanceolata* in the northern Rocky Mountains; the leaves of *C. lanceolata* var. *flava* have only the distinct midvein, whereas populations of typical *C. lanceolata* have leaves with two prominent lateral veins in addition to the midvein (Table 4).

TABLE 3. LOADINGS OF THE FIRST TWO PRINCIPAL COMPONENTS FOR THE QUANTITATIVE CHARACTERS MEASURED IN THE FIELD MORPHOLOGY STUDIES.

Character	Component 1	Component 2
Petal width	0.832	0.114
Leaf length	0.807	0.177
Height	0.789	0.033
Leaf length/width	0.755	−0.426
Sepal length	0.700	0.202
Petal length/width	−0.646	0.395
Leaf width	−0.189	0.847
Petal length	0.474	0.702

Davis (1952) also distinguished *C. lanceolata* var. *flava* from typical *C. lanceolata* by petal apex outline, describing the former as having petals "rounded at the apex," and the latter with petals "retuse or emarginate." Our studies confirmed that the petals of *C. lanceolata* var. *flava* are rounded at the apex, while those of typical *C. lanceolata* are usually retuse or emarginate (Table 4). In addition, the results of both the field and herbarium morphological studies confirmed that the petals of *C. lanceolata* var. *flava* are more nearly oval in shape, whereas those of *C. lanceolata* are most often obovate, and frequently narrowly so. These results also concur with the descriptions by Davis (1952).

Isozyme electrophoresis also clearly indicated that *C. lanceolata* var. *flava* is distinct from typical *C. lanceolata* and warrants recognition as a distinct species. The mean genetic identity between *C. lanceolata* var. *lanceolata* and populations representing *C. lanceolata* var. *flava* (I = 0.69) is close to the mean between congeneric species (I = 0.67) presented in several reviews (Gottlieb 1981; Crawford 1983). This value contrasts greatly with mean values for conspecific populations of var. *flava* (I = 0.91 to 0.98) and for populations of typical var. *lanceolata* (I = 0.89 to 0.99).

The diploid taxon represented by populations assignable to *C. lanceolata* var. *flava* includes conspecific yellow- and white-flowered plants. In this

TABLE 4. TAXON MEANS, RANGES AND STANDARD DEVIATIONS FOR QUANTITATIVE AND QUALITATIVE MORPHOLOGICAL CHARACTERS FROM HERBARIUM SPECIMENS, *CLAYTONIA LANCEOLATA* VARS. FLAVA, LANCEOLATA, AND MULTISCAPA, AND *C. ROSEA*. For some characters, the number of accessions was less than that shown in the first line; exceptions are given in parentheses after the means. * Petal apex outline scores: 0—retuse/emarginate, 1—rounded; ** Leaf venation scores: 0—lateral veins inconspicuous or absent, 1—lateral veins conspicuous.

	flava	*lanceolata*	*multiscapa*	*rosea*
No. of accessions	17	124	8	35
Leaf length (mm)				
Mean	41.6	32.6	43.4	44.0
Range	18–71	13–59	29–56	17.5–84
SD	3.1	0.9	3.7	2.8
Leaf width (mm)				
Mean	5.2	10.4	5.9	5.1
Range	2.4–8.4	2.8–26	2.3–10.6	1.3–14
SD	0.4	0.4	1.1	0.5
Leaf length/width ratio				
Mean	8.3	3.5	8.7	10.8
Range	4.7–15.1	1.7–12.5	5.2–13.0	4.0–32.8
SD	0.6	0.1	1.2	1.2
Sepal length (mm)				
Mean	4.4	3.8	4.8	4.7
Range	3.3–5.7	2.0–6.6	4.0–5.9	2.9–7.0
SD	0.2	0.1	0.3	0.2
Petal width (mm)				
Mean	4.3	4.0 (123)	4.6	4.1 (32)
Range	3.0–5.4	1.8–6.2	2.9–6.0	2.7–5.5
SD	0.2	0.1	0.3	0.1
Petal length (mm)				
Mean	9.5	9.1	9.2	9.3 (34)
Range	6.8–11.8	5.2–14.0	7.5–11.3	5.8–12.7
SD	0.3	0.1	0.6	0.3
Petal length/width ratio				
Mean	2.3	2.4 (123)	2.1	2.3 (32)
Range	1.5–3.1	1.6–3.7	1.3–2.6	1.5–3.2
SD	0.1	0.1	0.2	0.1
Petal/sepal length ratio				
Mean	2.2	2.4	1.9	2.1 (34)
Range	1.6–2.8	1.2–3.7	1.3–2.5	1.2–3.7
SD	0.1	0.1	0.1	0.1
Petal apex outline*				
Mean	0.9 (16)	0.1 (118)	1.0	0.9
Leaf venation**				
Mean	0.0	0.9 (123)	0.1	0.1 (34)

and other cases, flower color has been found to be of limited use in delineating true phylogenetic relationships within *Claytonia*. Elsewhere in North America, several other predominantly white- or pink-flowered taxa in *Claytonia* include named or unnamed yellow-flowered forms. Examples include *C. lanceolata* var. *chrysantha* (Douglas and Taylor 1972), *C. virginica* L. var. *hammondiae* (Kalmbacher) Doyle, Lewis and Snyder (Snyder 1992), and a recently discovered population of *C. caroliniana* in Maryland that contains yellow-flowered plants in addition to typical white- to pink-flowered plants (Snyder 1992). Such color forms are probably best viewed as minor variants within their respective taxa. They probably do not typically warrant taxonomic recognition, except in cases where their populations are correlated with ecological, genetic, geographic, and/or further morphological segregation (as is the case for *C. virginica* var. *hammondiae*) (Snyder 1992). In the case of *C. lanceolata* var. *chrysantha,* Douglas and Taylor (1972) found that, based on morphological, ecological, and biochemical analyses, "... there is no significant difference between the yellow and white forms of *Claytonia lanceolata,* other than petal color," and that "(t)he difference in petal color is most likely

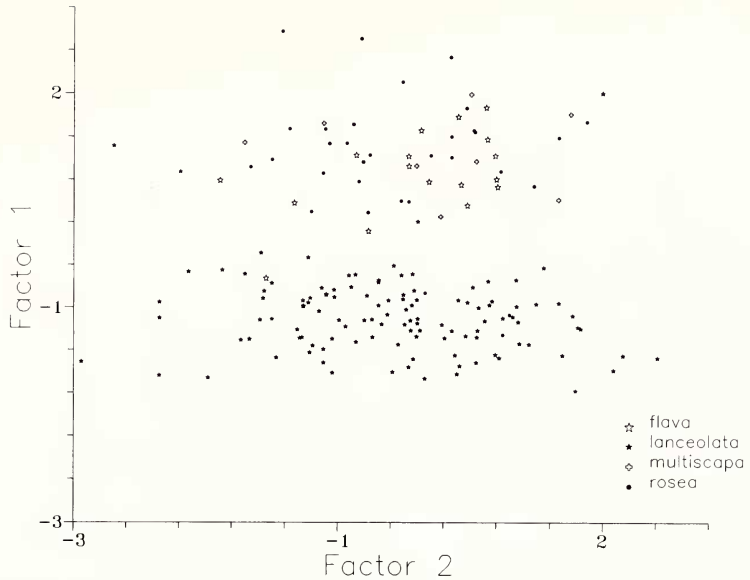

FIG. 3. Scatter diagram of individuals of *Claytonia rosea* and *C. lanceolata* vars. *flava, lanceolata* (including var. *chrysantha*), and *multiscapa* on principal components 1 and 2. Based on morphological data collected from herbarium specimens.

due to one or very few genes, as evidenced by the virtual lack of intermediate color forms." They concluded that "... there is no basis for the recognition of var. *chrysantha* ..." (Douglas and Taylor 1972). Our results indicate the same situation with respect to the yellow and white flower color phenotypes of "*C. lanceolata* var. *flava.*" Plants of the two color phenotypes are biotically sympatric in at least four populations in the northern Rocky Mountains, and these phenotypes reflect little or no morphological or isozyme differentiation within or among those populations. While there was some genetic differentiation among populations of *C. lanceolata* var. *flava,* plants of the two flower color phenotypes are undoubtedly conspecific; at the four sites where they are biotically sympatric, individuals of the two phenotypes are nearly or completely identical genetically. This suggests that in such cases they are part of the same breeding population, that flower color represents simple genetic differences (i.e., determined by one or a few genes), and that flower color does not warrant taxonomic recognition. The allozyme data also suggest separate origins of the yellow flower phenotype in each locality where it occurs.

TABLE 5. LOADINGS OF THE FIRST TWO PRINCIPAL COMPONENTS FOR THE QUANTITATIVE AND QUALITATIVE CHARACTERS USED IN THE HERBARIUM MORPHOLOGY STUDY.

Character	Component 1	Component 2
Venation	−0.840	0.039
Petal apex outline	0.830	−0.051
Leaf length/width	0.775	−0.061
Leaf width	−0.630	0.472
Petal/sepal length ratio	−0.607	0.121
Sepal length	0.588	0.450
Petal width	0.069	0.872
Petal length	−0.095	0.778
Leaf length	0.344	0.500
Petal length/width	−0.174	−0.409

The morphological comparison among species of *Claytonia* revealed a strong similarity between *C. rosea* and *C. lanceolata* vars. *flava* and *multiscapa* (Fig. 3). The latter variety, all collections of which are white-flowered, is reported by Hitchcock et al. (1964) as occurring in "Yellowstone National Park and vicinity." The morphological similarity of var. *multiscapa* to var. *flava,* and its complete geographic overlap with stations of white- and/or yellow-flowered populations of the latter entity, support the notion that var. *multiscapa* is the same taxon as the white-flowered form of var. "*flava.*" The more southerly white- to pink-flowered *Claytonia rosea* probably represents a similar, closely related narrow-leaved taxon (J. Miller personal communication). Like the populations of *C. lanceolata* var. *flava* sampled in Montana and Wyoming, numerous Colorado populations of *C. rosea* are diploid (n=8; Halleck and Wiens 1966).

In summary, electrophoretic and morphological data clearly revealed that *C. lanceolata* var. *flava* does not belong in the *C. lanceolata* complex. Rather, its affinities lie with the narrow-leaved group of species that includes *C. rosea, C. tuberosa* Pallas ex Willd. and *C. virginica.* Furthermore, *C.*

TABLE 6. ALLELE FREQUENCIES AT 19 ENZYME LOCI FOR 14 POPULATIONS OF *CLAYTONIA LANCEOLATA*. [1] = white-flowered phenotype of *C. lanceolata* var. *flava* is not represented at Hebgen Lake. [2] y = yellow-flowered phenotype of *C. lanceolata* var. *flava*; w = white-flowered phenotype of *C. lanceolata* var. *flava*; lanc = *C. lanceolata* var. *lanceolata*. [3] = number of individuals per taxon or flower color morph sampled at each location.

		Study locations													
		Hebgen Lake[1]		Anaconda			Champion Pass			Wyoming			Vipond Park		
Locus	Allele	y[2] 50[3]	lanc 50	y 50	w 50	lanc 50	y 50	w 30	lanc 49	y 50	w 50	lanc 50	y 30	w 40	lanc 30
Mdh-1	a	0	0	0	0	0.02	0	0	0	0	0	0	0	0	0
	b	0	0.81	0.05	0.01	0.98	0.08	0.10	0.98	0	0	1.00	0.10	0.06	1.00
	c	1.00	0.19	0.95	0.99	0	0.92	0.90	0.02	1.00	1.00	0	0.90	0.94	0
Mdh-2	a	0	0	0	0	0.01	0	0	0	0	0	0	0	0	0
	b	1.00	1.00	1.00	1.00	0.99	1.00	1.00	1.00	1.00	100	1.00	1.00	1.00	1.00
Mdh-3	a	0	0.06	0	0	0	0	0	0.21	0	0	0.18	0	0	0
	b	0	0.94	0	0	1.00	0	0	0.64	0	0	0.65	0	0	1.00
	c	1.00	0	0.96	0.97	0	1.00	1.00	0.15	1.00	1.00	0.11	0.95	0.97	0
	d	0	0	0.04	0.03	0	0	0	0	0	0	0.06	0.05	0.03	0
Pgm-1	a	0.90	1.00	1.00	1.00	1.00	0.62	0.53	1.00	1.00	1.00	1.00	1.00	0.97	1.00
	b	0.10	0	0	0	0	0.38	0.47	0	0	0	0	0	0.03	0
Pgm-2	a	0.64	0.01	0	0	0	0	0	0.04	0.55	0.54	0	0	0	0
	b	0.10	0.65	0.75	0.90	0.37	0.88	0.93	0.46	0.06	0.06	0.18	0.27	0.42	0.40
	c	0.26	0.21	0.06	0.03	0.57	0.03	0.02	0.48	0.39	0.42	0.77	0.52	0.18	0.49
	d	0	0.13	0.19	0.07	0.06	0.03	0.05	0.02	0	0	0.05	0.21	0.40	0.11
G3pdh	a	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
Lap	a	0	0.01	0	0	0.03	0	0	0	0	0	0.08	0	0	0.06
	b	1.00	0.36	1.00	0.95	0.87	0.99	1.00	0.97	1.00	1.00	0.44	0.98	1.00	0.55
	c	0	0.63	0	0.05	0.10	0.01	0	0.03	0	0	0.48	0.02	0	0.39
Aat	a	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
Adh	a	0	0	0	0	0.01	0.02	0	0	0.46	0.36	0	0	0.02	0
	b	1.00	0	1.00	0.98	0.28	0.98	1.00	0.02	0.54	0.64	0.10	0.98	0.94	0
	c	0	1.00	0	0.02	0.71	0	0	0.98	0	0	0.90	0.02	0.04	1.00
Pgi-1	a	1.00	1.00	1.00	0.99	1.00	1.00	0.98	1.00	1.00	1.00	1.00	1.00	1.00	1.00
	b	0	0	0	0.01	0	0	0.02	0	0	0	0	0	0	0
Pgi-2	a	0	0.04	0	0	0.01	0	0	0.02	0	0	0.05	0	0	0.06
	b	0.04	0.44	0.32	0.29	0.55	0.12	0.07	0.55	0.31	0.39	0.70	0.02	0.06	0.43
	c	0.96	0.52	0.68	0.71	0.44	0.88	0.93	0.43	0.69	0.61	0.25	0.98	0.94	0.51
Tpi-1	a	0.01	0.01	0.06	0.06	0.01	0	0	0	0	0	0	0.05	0	0
	b	0.81	0.71	0.91	0.92	0.81	0.91	0.87	0.96	0.92	0.86	0.99	0.93	0.96	0.96
	c	0.15	0.28	0.03	0.02	0.18	0.09	0.13	0.04	0.08	0.14	0.01	0.02	0.04	0.04
	d	0.03	0	0	0	0	0	0	0	0	0	0	0	0	0
Tpi-2	a	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
Tpi-3	a	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
Mnr	a	0	1.00	0	0	1.00	0.02	0	0.46	0.07	0.20	0.98	0	0	0.89
	b	0.94	0	0.53	0.50	0	0.52	0.55	0.54	0.93	0.80	0.02	0.27	0.39	0.04

TABLE 6. CONTINUED

Locus	Allele	Study locations															
		Hebgen Lake[1]		Anaconda			Champion Pass			Wyoming			Vipond Park		
		y[2] 50[3]	lanc 50	y 50	w 50	lanc 50	y 50	w 30	lanc 49	y 50	w 50	lanc 50	y 30	w 40	lanc 30
	c	0.06	0	0.47	0.50	0	0.46	0.45	0	0	0	0	0.73	0.61	0
	d	0	0	0	0	0	0	0	0	0	0	0	0	0	0.07
Skdh	a	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
6pgd-1	a	0.22	0	0.51	0.55	0	0.41	0.63	0	0.23	0.20	0	0.58	0.58	0
	b	0.78	0	0.49	0.45	0	0.59	0.37	0	0.76	0.79	0.10	0.40	0.42	0.53
	c	0	1.00	0	0	1.00	0	0	1.00	0.01	0.01	0.90	0.02	0	0.47
6pgd-2	a	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.94	1.00	1.00	1.00
	b	0	0	0	0	0	0	0	0	0	0	0.06	0	0	0
Idh	a	0	0.03	0	0	0.13	0	0	0.05	0	0	0	0	0	0.07
	b	0	0.97	0	0	0.87	0.35	0.31	0.95	0	0	1.00	0	0	0.93
	c	0.98	0	0.99	1.00	0	0.65	0.69	0	0.91	0.95	0	0.75	0.77	0
	d	0.02	0	0.01	0	0	0	0	0	0.09	0.05	0	0.25	0.23	0

lanceolata vars. *flava* and *multiscapa* would best be treated conspecifically as *C. multiscapa* (J. Miller personal communication); such a proposed treatment is supported by the results of our herbarium morphological study, as well as the entirely overlapping geographic ranges, of the plants currently bearing these names from the Yellowstone and surrounding areas. Formal nomenclatural changes are not made here, but left for publication of a complete revision of the genus (Miller and Chambers in mss.).

Conservation status. In the northern Rocky Mountains, narrow-leaved populations of *Claytonia* consisting wholly or partially of yellow-flowered individuals remain relatively uncommon (ten such populations are now known from Idaho, Montana, and Wyoming). However, the morphologically and allozymically highly similar white-flowered populations are more common and widespread. These white-flowered populations occur over a larger area in northwestern and north-central Wyoming, and south-central to southwestern Montana; a population has also recently been confirmed in the Sweetgrass Hills of north-central Montana (B. Heidel personal communication). Populations of both flower color phenotypes are usually very large in size and areal extent, and at least 30 populations consisting of one or both forms have been documented in Montana (Montana Natural Heritage Program unpublished data). Because these yellow and white flower color phenotypes are "contaxonomic," *C. lanceolata* var. *flava* is not in need of protective listing, regardless of its eventual taxonomic disposition.

When necessary, legal protection and management of putatively endangered taxa should be preceded by accurate evaluations of their phylogenetic relationships and taxonomic status (Avise and Nelson 1989). Biochemical and molecular techniques will continue to be increasingly useful for ensuring that the limited funds available for endangered species conservation are correctly focused on evolutionarily deserving taxa in the endeavor to maintain biological diversity.

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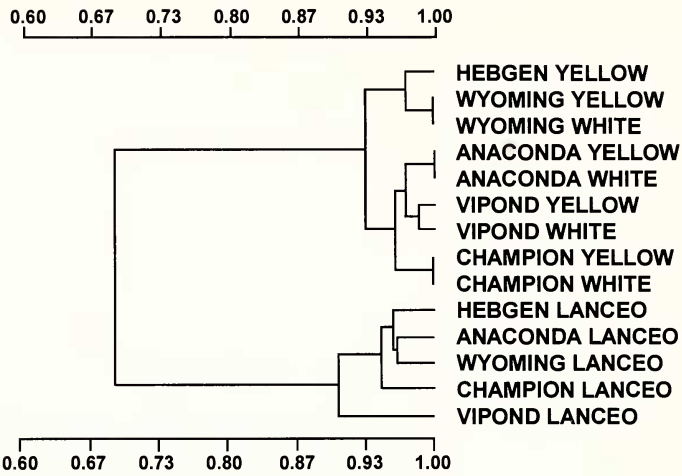

FIG. 4. Phenetic relationships among populations of *Claytonia lanceolata* var. *flava* (yellow- and white-flowered) and *C. lanceolata* var. *lanceolata,* based on cluster analysis (UPGMA) of Nei's genetic identity values.

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